THE ECOLOGICAL RELATIONS OF THE VEGETATION ON THE SAND DUNES OF LAKE MICHIGAN.

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[*Continued from p. 202.*]

3. *Encroachment on preexisting plant societies.*

THOSE who are at all familiar with wandering dunes are acquainted with their power to destroy vegetation in the path of their advance. This, indeed, is to many people the most conspicuous feature of a sand dune area, because it often becomes a feature of the greatest economic importance. The effect of an advancing dune upon the preexisting vegetation varies greatly as conditions vary. The most important factors are the rate of advance, the height of the advancing dune above the territory in its path, and the character of the vegetation that is encroached upon.

The rate of advance is, of course, a decidedly variable factor, since all rates, from nothing up to the maximum rate, may be found along nearly all advancing lee slopes. At a given point the rate varies greatly during different seasons. An advancing portion may become checked and a checked portion may advance again, as wind-sweeps are clogged up or opened once more. The multiform changes on the complex, each and all, affect the rate of advance to a remarkable degree. Attempts have been made to measure the maxima of advance at Dune Park, but a sufficient time has not elapsed as yet to allow of any satisfactory conclusions. In November 1897 a stake was driven at the basal edge of a rapidly advancing lee slope. The height of this stake above the ground was a little more than a meter. In May 1898 the stake was nearly covered, and it could not be found at all in July. At this point, therefore, the vertical component of advance amounted to a meter in six months; the horizontal component, of course, was greater still,

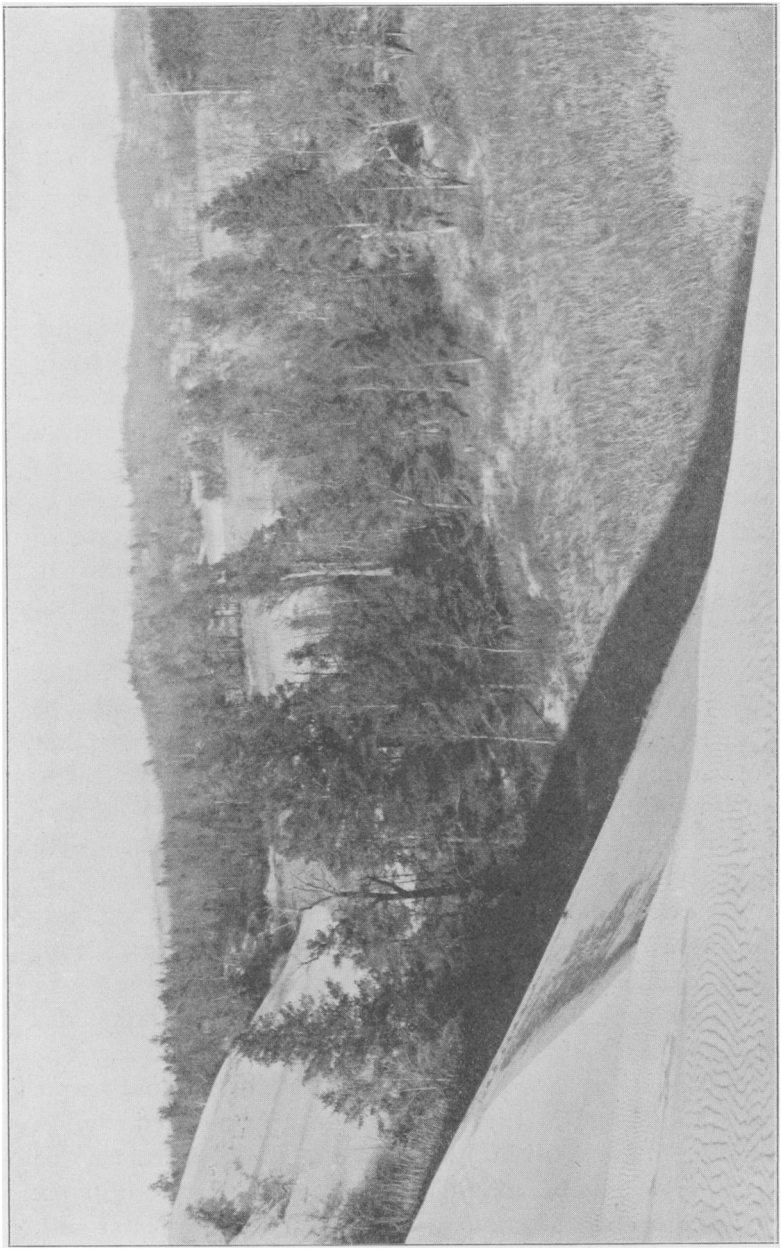

FIG. 9.—General view at Dune Park, showing the encroachment of a dune on pools, swamps, and forests. Dune crest in the left background, oak dunes at the right. Wind ripples in the foreground. View taken in winter.

FIG. 10.—A doomed forest of basswoods, etc., at Dune Park. Dunes encroaching from all sides, but somewhat slowly; dune at right advancing in the direction of the prevailing wind. Thicket of basswood, dogwood, etc., at the left background. Subsequent vegetation in the foreground (grape at right, chokecherry at left).

since the angle of slope was about 30°. The general statement may be made for the Dune Park complex that the maxima of advance are to be measured in decimeters or meters per annum, rather than in centimeters or decameters. No estimates can be given for other localities. In all probability the Glen Haven dunes move more slowly, since the slopes have a much richer vegetation.

The height of an advancing dune above the territory in front of it is a very important factor, inasmuch as it often determines the life or death of a flora. At Glen Haven, where the advancing dunes are from thirty to sixty meters high, no preexisting vegetation can survive the burial which awaits it. At Dune Park, where the crest is never as much as thirty meters high, vegetation sometimes survives. This survival is determined chiefly by the nature of the vegetation, and the succeeding paragraphs will have to do with the struggle between dunes and floras at Dune Park.

The advancing dunes at Dune Park encroach now upon a swamp, now upon a forest. *Fig. 9* shows how these forest and swamp conditions alternate. In the right foreground is a pool, surrounded by bulrushes. Toward the center of the photograph there is a ridge tenanted by pines and oaks, then another swamp and another ridge. *Fig. 10* shows a very interesting phenomenon. At the center is a deep trough, surrounded on all sides by advancing dunes. This trough has never been a wind-sweep, but was made by the piling of the sand all about it. The flora in this depression is not a typical sand-dune flora, although surrounded by such on all sides. It is a mesophytic island in a xerophytic sea. The dominant trees in this little group are the basswood, *Tilia Americana*, and the ash, *Fraxinus Americana*. Although the basswood is common on the arrested dunes, this plant society is quite evidently a relict of a larger area developed under more genial conditions. The lake is toward the right, and the dune on that side is advancing with some degree of rapidity. The dune to the left is pushed forward in the main by the action of southerly winds, and moves quite

slowly. This dune, however, is at the upper end of the curved wind-sweep previously mentioned, so that northwest winds contribute to its advance. Thus it becomes possible for the same wind to cause the advance of two dunes toward each other and hasten the burial of a flora. The advance of all dunes at this point is relatively slow, as is shown by the comparatively abundant vegetation on the advancing slopes. This vegetation is not a relict of the past. The advancing dunes completely destroy all of the preexisting vegetation at this point. In a few more years, unless conditions change, there will be nothing left at the surface by which one may interpret the history of this dying plant society.

The encroachment of a dune upon a forest is shown in *figs. 11* and *12*. The forests in this vicinity consist principally of the scrub pine, *Pinus Banksiana*, and the black oak, *Quercus coccinea tinctoria*. Neither of these trees can survive any such degree of burial, as can the cottonwood. The oak, especially, succumbs long before the entire tree is buried; the dead trees along the dune margin in both pictures are oaks. *Fig. 12* shows a pine that is half buried, but apparently as vigorous as ever. The dead trees in *figs. 15* and *16* are mostly scrub pines, and they seem to show no greater adaptation to their new surroundings than do the oaks. There appears to be a wide range of individual adaptation in pine trees, some dying almost as soon as the dune reaches them at all, while others are nearly as resistant as the cottonwood. In both pines and oaks the first obvious sign that the tree is waging a losing struggle is etiolation. The living trees along the margin (as in *figs. 11* and *12*) rarely have a dark green foliage. In most cases the leaves are yellowish green, and in some cases almost white. Nor are the leaves as numerous or large as on healthy trees.

Such tree groups, as are shown in *figs. 9*, *10*, *13*, and *14*, are doomed to an inevitable death. The length of life allotted to them in the future depends almost entirely upon the rate of the dune's advance. There are some evidences in favor of the view that an individual pine tree can endure a deeper covering before

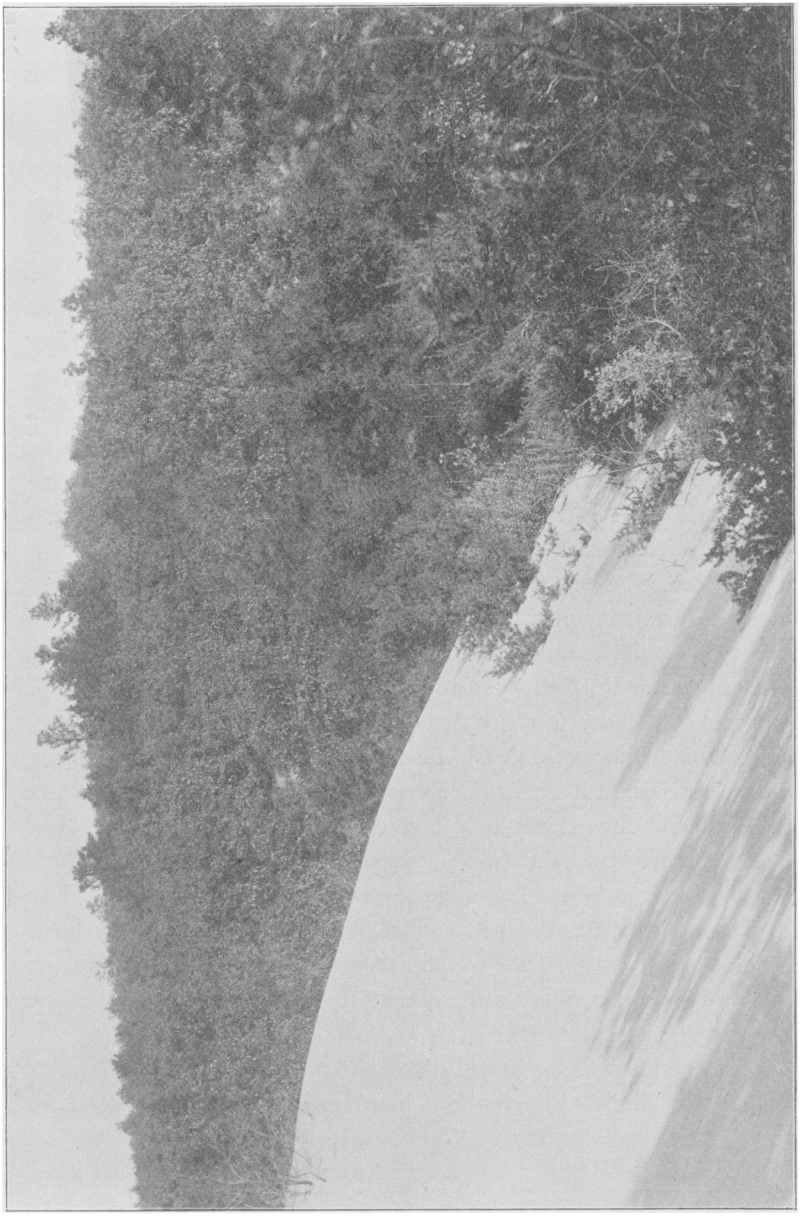

FIG. 11.—Encroachment of a dune on an old and long-established oak dune at Dune Park. Dead oak trees at the margin.

FIG. 12.—Encroachment of a dune upon an oak forest at Dune Park. Bugseed in the left foreground. Half buried but vigorous pine at the center. Dead oak trees at the margin.

death ensues, if the rate of advance is slow. *Fig. 12*, which represents a half buried pine that is still vigorous, was taken at a point where the advance is relatively slow. *Figs. 15* and *16*, on the other hand, where the pines were soon killed, represents one of the most rapidly advancing dunes at Dune Park. Thus the individual adaptation referred to in the preceding paragraph may be in part delusive. Perhaps the trees are able to adapt themselves more fully, and hence undergo a greater degree of covering before they die, where the advance of a dune is comparatively slow. Sometimes (as in *fig. 11*) the territory toward which the dune advances is higher than the dune itself. In such a case the advancing dune is checked. If the entire area in front is higher than the dune, the sand gradually accumulates until the altitude is great enough to permit another advance. When, however, a ridge meets the advancing dune at right angles (as in *fig. 9*), the dune's course is deflected to either side. If the ridge is high enough, some of the trees may be able to escape the fate of their associates. The pines in the background of *fig. 17* probably represent a portion of the flora at the top of one of these ridges.

At Glen Haven, as has been stated, the forest vegetation readily succumbs, because of the great height of the advancing dune. The forests are mainly of two types, the maple or the arbor vitae. The maple forests have a dominance of *Acer saccharinum*, and represent the most common type of mesophytic forest in that part of Michigan. The arbor vitae forests are in reality swamp forests, and the most typical trees present there are *Thuya occidentalis*, *Betula papyrifera*, and *Fraxinus Americana*. The line of dead trees along the margin of the advancing dune (as shown to a slight extent in *figs. 11* and *12*) is particularly striking where there is an encroachment upon a maple forest. Sometimes the hemlock, *Tsuga Canadensis*, grows with the maple and shares its fate. At one point the dune encroaches upon a forest of *Pinus Banksiana*, and the results are precisely as at Dune Park.

Dunes that are encroaching upon forests may be found along

the entire coast, though their best development is in association with an extensive dune-complex, as at Dune Park or Glen Haven. The burial of forests was observed at Frankfort, Muskegon, and elsewhere, and is a relatively common phenomenon. In closing up the treatment of the forests, the general statement may be made that an advancing dune destroys the entire forest vegetation. Where this rule meets with any exception, it is an exception that in no real sense invalidates the main proposition.

The encroachment of a dune upon a swamp is of less common occurrence than encroachment upon forests, because forests are so much more common than swamps along the lake shore. The best examples of dunes advancing on swamps were seen at Dune Park, where there are a number of swamps that run more or less parallel with the lake shore. *Fig. 9* gives a good impression of the general appearance of things in the vicinity of Dune Park. In the foreground is a pool and bulrush swamp upon which the dune is encroaching. Beyond the wooded ridge at the center is another swamp of the same type, which is suffering the same fate. In the distance there can be seen the crest of a dune, which is advancing upon a chain of forest-clad hills.

The dune which is shown in the foreground of *fig. 9* encroaches upon a pool in which there is an abundance of aquatic plants, such as *Nymphaea odorata*, *Nuphar advena*, and *Pontederia cordata*. These plants are soon destroyed, of course, but it is surprising how long it is before they die. Leaves of Nymphaea and Nuphar have often been seen raised above the sand, a meter back of the present margin of the pond. These plants must have been partially buried for some weeks, and yet the leaves were scarcely blanched at all. Indeed, an oak tree buried to an equal relative depth would have succumbed entirely. Around the margin of the pool is a luxuriant growth of the bulrush, *Scirpus lacustris*. This plant soon gives up the struggle, etiolation being present when only the basal portion of a stem is buried. The appearance of the bulrush is often striking by reason of the fact that there are etiolated rings alternating with green rings of stem tissue.

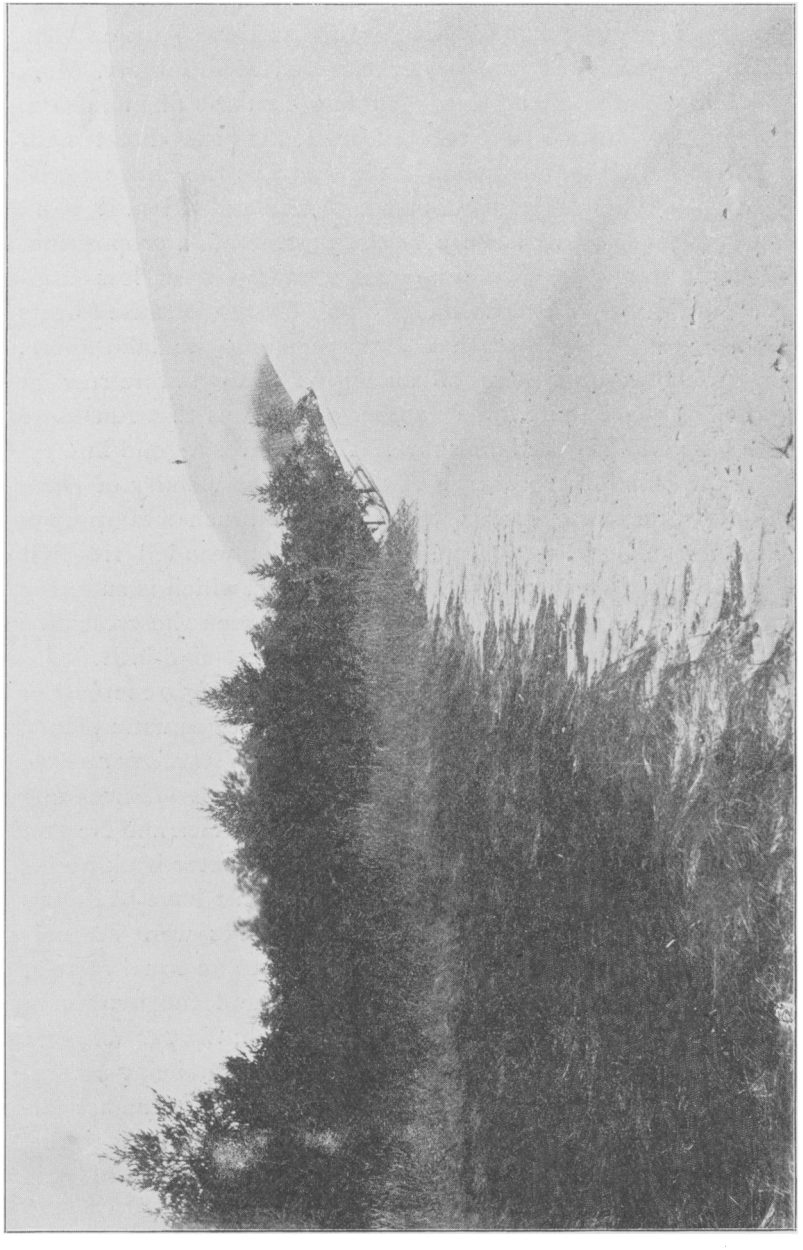

FIG. 13.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a sedge swamp and pine bottom. Complete destruction of preexisting vegetation. Beachlike fringe of moist sand at the base of the dune.

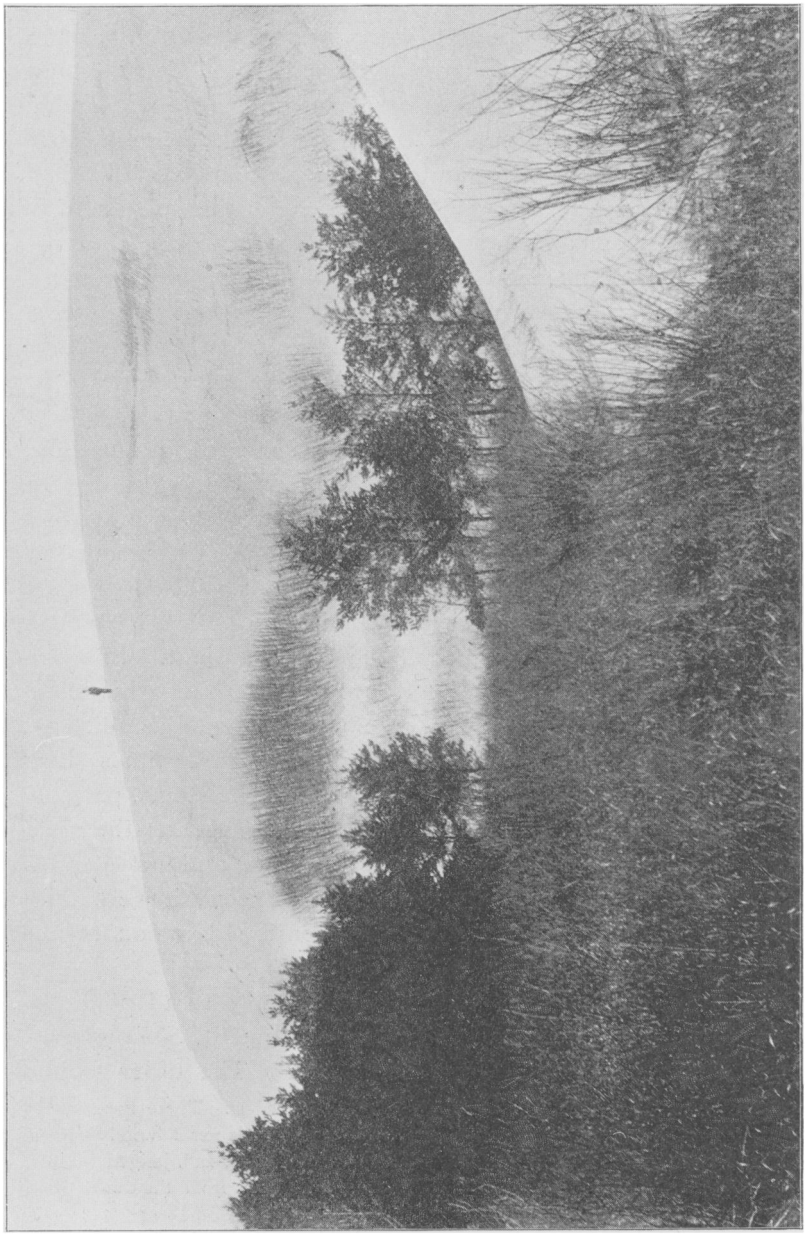

FIG. 14.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a swamp and pine bottom. Pocket in the dune with pines. Dogwoods on the slopes. View taken in winter.

Fig. 13 shows the encroachment of a low dune upon a sedge swamp. The beachlike fringe of sand at the base of the dune is peculiar to dunes that encroach on swamps. Considerable sand rolls or is blown beyond the base of the steep slope. Under ordinary conditions this sand is blown away, but as soon as it reaches the wet, swampy ground, it becomes moist, and hence remains for a time as a fringe to the dune. The plants of a sedge swamp are unable to adapt themselves to a dune environment, and quickly succumb. *Fig. 14* shows a dune advancing on a more mesophytic flora and on a group of pines. The effect here is also destructive, in the main. An interesting pocket in the dune, in which there is a group of pine trees, appears in this figure.

One of the most remarkable phenomena seen in the dune region is shown in *fig. 15*. A dune about twenty five meters in height is advancing with considerable rapidity upon a bulrush swamp. This swamp is more or less continuously surrounded by a marginal fringe of willows and dogwoods. The bulrushes are quickly destroyed, but the dogwoods and willows have thus far been able to remain not only alive but luxuriant. In order to keep above the sand, these plants are obliged to lengthen their stems far more than is ever the case under normal conditions. Already some of these plants have twice and three times their normal stem height. The buried portions of the stems, particularly of the willows, send out roots almost as soon as they are buried. These plants, therefore, become more and more independent of the deeper soil in which they first grew, thus escaping one of the greatest dangers that was mentioned in connection with many tenants of the embryonic dunes.

Three species have been found that are able to adapt themselves almost immediately to a dune environment, *Salix glaucophylla*, *S. adenophylla*, and *Cornus stolonifera*.[3] The taller shrubs

[3] Some of the *Cornus stolonifera* may prove to be *C. Baileyi*. These two species certainly intergrade in the dune region. The pubescence character is largely a question of habitat. The best determinative character is the stone, and, judged by this, nearly all specimens examined, whether from the swamps or from the dunes, were *C. stolonifera*. See BOT. GAZ. **15**: 38, 86–88. 1890.

in *fig. 15*, as at the left of the center, are *Salix adenophylla*. The lower shrubs are dogwoods or glaucous willows. *Fig. 16* shows a group of the latter two species growing together. How long these plants will be able to endure is a question that cannot now be answered. The conditions become severer each year, because of the necessity for increased stem elongation, and also because the plants are constantly rising above the protected position in the lee of the dune. At no place is the destructive action of the wind greater than at the summit of an advancing lee slope.

The encroachment of a dune upon an open swamp or a body of water is seen occasionally along the Michigan shore, as at Grand Haven. In no case, however, were any facts obtained that added anything essential to those given above. In concluding the section on dune encroachment, it may be said that the only conspicuous case of the survival of members of a preexisting flora is furnished by the swamps. It may at first seem a surprising fact that the plants which are able to adapt themselves to the intensely severe conditions of an advancing dune are hydrophytic willows and dogwoods, rather than mesophytic oaks, basswoods, and maples, or xerophytic pines. Such a view as this comes from a misconception of the change that is needed in the life-habits of the plant. The relation to the soil water is not conspicuously altered, or at least not rapidly altered. It is true that the elongating stem makes it more and more difficult for the plant to draw water from the original root system; but in the case of the willow, at any rate, this is counterbalanced by the development of new roots along the buried stem, which allow the plant to utilize the moisture in the sand. The trees mentioned above are unable to send out such roots, and here, at least, is one possible source of their failure.

There is another line along which the solution of this problem of adaptation may be sought. A number of ecologists in later years have commented on the xerophytic structures of many swamp plants. These structures are not to be found in all swamp plants, but are particularly well-marked in plants of

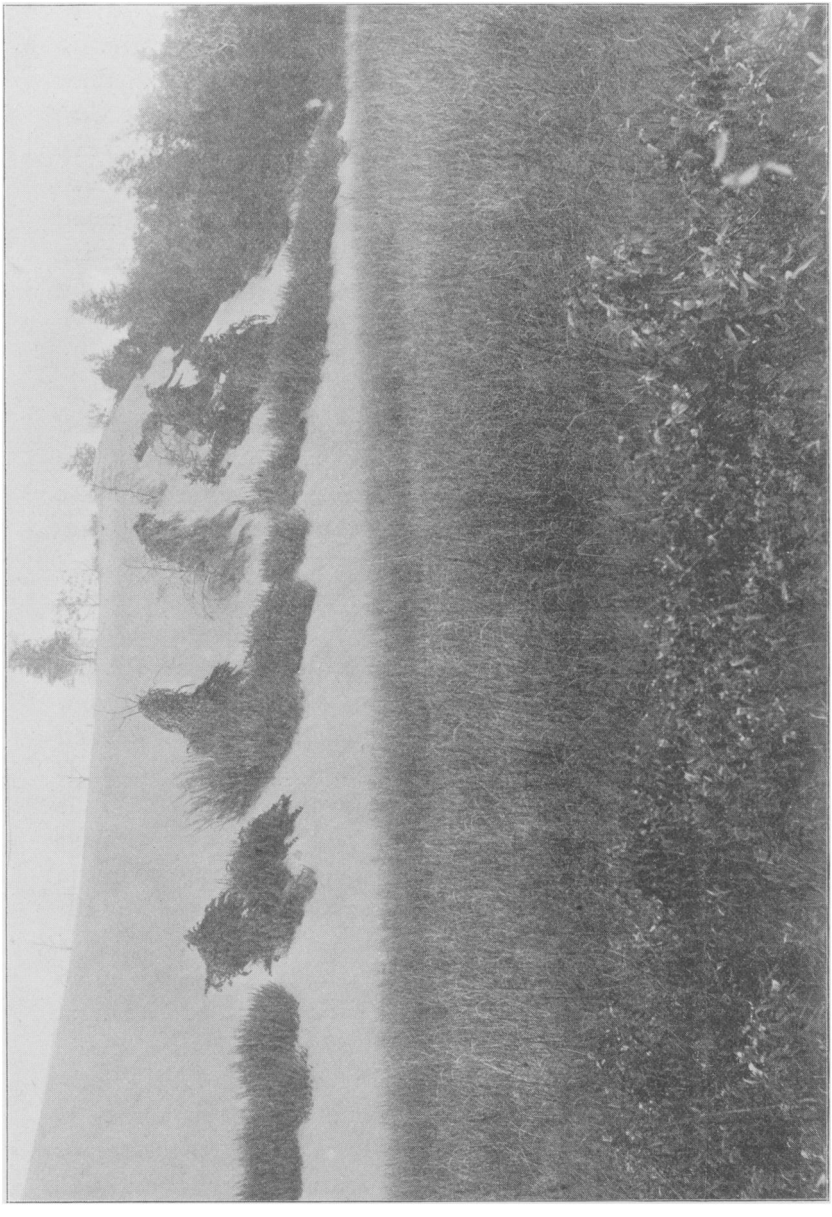

FIG. 15.—Steep lee slope of a rapidly advancing dune at Dune Park. Encroachment on a bulrush swamp, which has a marginal row of willows and dogwoods. Death of the herbs and pines, but survival of the shrubs through vertical elongation, enabling them to rise above the sand.

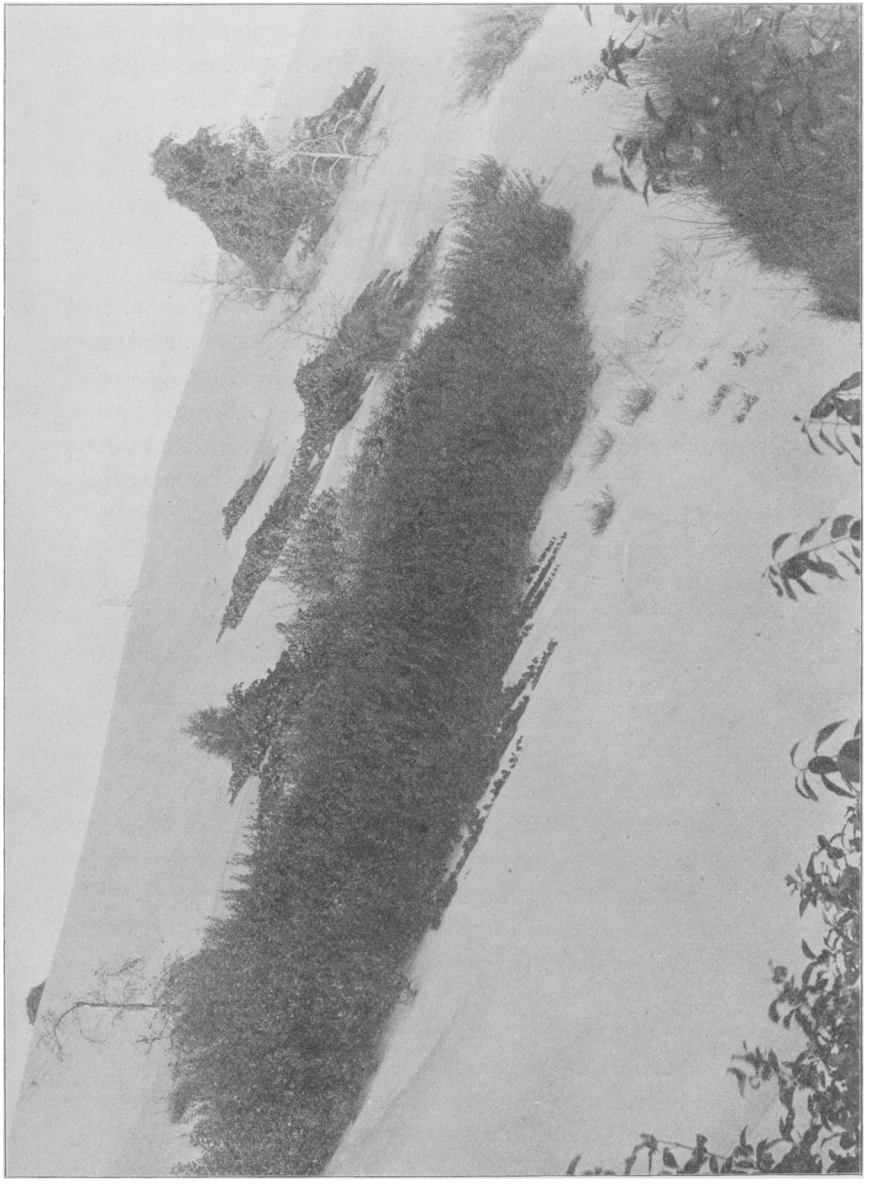

FIG. 16.—Section of the lee slope shown in *fig. 15*. Dogwood and glaucous willows at the center (antecedent). Scattered dead pines. Subsequent vegetation consisting of trailing and climbing grapevines, cedar, and bugseed.

undrained swamps, *e. g.*, peat bogs. Schimper even goes so far as to regard peat bog plants as xerophytes, because the humus acids in the soil make it difficult for plants to obtain the requisite amount of water. Consequently peat bog plants have worked out xerophytic structures to reduce the transpiration. All of the swamps at Dune Park are undrained swamps, and may be called potential peat bogs. The chemical nature of the soil is such that the plants have doubtless adapted themselves to all of the essential conditions of a xerophytic life. The partial burial of these plants by a dune results, as has been seen, in no rapid change of relations with the water in the soil. The aerial organs, however, are exposed to a greater degree of light and heat by reason of their proximity to the sand. Thus the tendency to transpiration is increased, but the plants may be able to keep it within bounds through the xerophytic structures that have already been worked out in a swamp environment. It is likely, too, that these structures become more and more xerophytic as a result of life on and in the dune.

The theories that have been exploited in the preceding paragraph find, at least, a partial confirmation. The leaves of the three successful species have more or less pronounced xerophytic structure. The leaves of the dogwood are quite strongly pubescent. The willows, however, are more decidedly xerophytic. The leaves of *Salix adenophylla* are very hairy, and the cuticle is thick. *Salix glaucophylla* has leaves with a very thick cuticle, and coated on the under surface with a dense layer of bloom. In the dune form of this latter species the leaves are notably thicker and the bloom more dense. It is the author's intention to make a careful comparative study of the anatomical characters of these plants, and make report in the second part of this paper. All three of the species named above have a remarkably wide range of habitat, occurring on embryonic dunes, arrested dunes and heaths, as well as in swamps and on lee slopes. These shrubs may grow at almost any altitude and show a surprising independence of the water level in the soil. There seems to be scarcely any doubt, therefore, but

that these species are naturally adapted to a xerophytic life, and that, when the occasion arises, still further xerophytic conditions can be met successfully.

The success of the willows and dogwoods on the dunes may be due, in part, to yet another characteristic. It is well known that swamp plants are provided with extensive adaptations to promote aeration. This need is especially apparent in undrained swamps, where the gases necessary for the underground tissues and organs have to be almost entirely supplied from above the surface of the soil. It is in these undrained swamps, too, that the accumulation of peat is so rapid. It seems rational, then, to suppose that tenants of undrained swamps, by adapting themselves to prevent suffocation, have also adapted themselves to withstand burial by sand without injury. Just what is the cause of death, when plants are partially buried by the soil, is, so far as the author knows, an unanswered question. A wide field for anatomical study and physiological experiment lies open along this line. In the meantime the notion that plants of undrained swamps are better fitted to suffer partial burial than are other plants may remain as a tentative theory.

In considering the formation of secondary embryonic dunes, mention was made of *Potentilla Anserina*, *Cephalanthus occidentalis*, and *Polygonum Hartwrightii* as dune-formers under certain conditions. Potentilla and Polygonum are extensively creeping herbs, while Cephalanthus is an erect shrub. All three are swamp plants naturally, and yet able, as has been said, to build low dunes of a slow growth. In like manner they sometimes remain living for a time when a wandering dune encroaches upon them. They are especially plastic where the advance of a dune is relatively slow. Among these plants Potentilla seems to be the most adaptable to dune conditions. Another swamp plant that shows a surprising degree of plasticity is *Hypericum Kalmianum*. This shrub is very common in the undrained swamps of the dune region, and very often finds itself in the path of an advancing dune. Hypericum, like Salix, often forms a marginal fringe about a swamp, and miniature lines of this shrub are

frequently to be seen toward the base of an encroaching dune, resembling the line of willows and dogwoods shown in *fig. 15*. Of course, Hypericum has nothing like the plasticity and endurance of Salix; nevertheless it may live for many years if the dune advances slowly. Its capacity for vertical elongation is much less than that of Salix or Cornus, so that a rapid advance would soon cover the plants and cause their death. Near the South Chicago beach is a pool with a dense vegetation of *Scirpus pungens* about its margin. This plant has served to collect a small amount of sand, and is forming a low secondary dune. Although a large portion of each shoot is covered by the sand, there is as yet no sign of etiolation on the aerial parts of the plant.

Since the highest portion of a wandering dune is close to its advancing front, it is evident that a buried forest will gradually become uncovered, as the dune passes on beyond. No scene in all the dune area is more desolate than such a place. It is a veritable graveyard, where the corpses once buried are exposed again. *Fig. 17* shows a pine graveyard which has had a history like this. In the background are several living pines, presumably members of the same forest with the others. Their position at the summit of a hill permitted them to survive, while those at lower levels were buried by the sand. The uncovered pine trunks are directly in the path of the main wind currents, and hence are subjected to the severest action of the sand-blast. The trunks are carved and battered away until the last remnant of the old vegetation passes away forever.

Graveyards similar to those at Dune Park occur on the extensive dune-complex at Glen Haven. The commonest dead tree there appears to be the arbor vitae, though there are occasional dead trees of birch and ash. In addition to the trunks of trees, there is an abundance of resurrected soil lines at all altitudes on the complex. These black streaks in the sand vary greatly in depth and persistence. Doubtless the organic matter thus exposed is sometimes utilized by the scanty vegetation on the complex, but more commonly it is rapidly scattered by the winds.

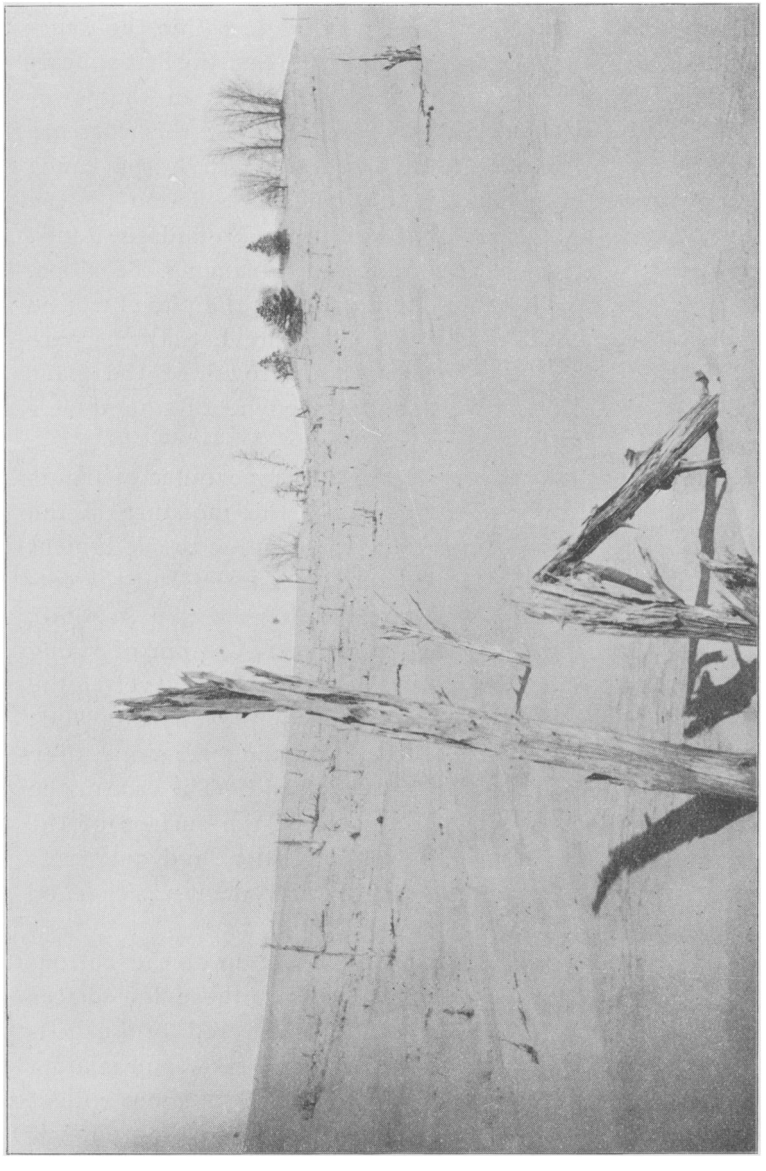

FIG. 17.—Pine graveyard at Dune Park. Forest once buried and destroyed; the dead trees now exposed again. Surviving members of the old pine forest in the background. This area is now a gentle windward slope, and has been converted into a wind-sweep. Carving and battering of the old trunks by sand-blast.

4. *Capture of the dune-complex by vegetation.*

The capture of a dune by plants may begin within the dune-complex itself or along its margin. In either case the first appearance of the advancing vegetation is commonly in the lower places toward the water level. The reasons for this fact are obvious. These low places are well protected from the wind; there is no danger, therefore, of any sand-blast action on the plant organs nor any removal of soil from around the roots. When the growth begins at the foot of an advancing lee slope, there is, however, considerable likelihood that the plants will be covered by the sand. It is this fact which prevents the capture of a rapidly advancing dune; the vertical growth of the plant must be greater than the vertical component of the dune's advance.

The most important reason for the first appearance of plants at lower levels is the soil moisture. It is the moisture at the surface of the soil which causes to a large degree the lodgment of seeds, and especially light cottony seeds like those of the cottonwood and willow. At the base of the dune shown in *fig.* 9, where it is encroaching on a swamp pool, there is a line of young cottonwoods and willows several inches above the level of the pool. The seeds were blown across the complex by the wind; when they reached the crest of the advancing lee slope, they rolled down to the base together with the sand. The base of the dune is always moist several inches above the surface of the water because of capillarity. As soon as the sand and seeds reached the moist soil near the base, the movement was checked and both found lodgment.

The moisture necessary for the germination of the cottonwood and willow seeds is also furnished at these low places near the water level. The danger of being covered by the drifting sand is much less at this place because moist sand is more compact than dry sand, and because moist sand does not collect about the growing plants. The dune shown in the foreground of *fig.* 9, however, is advancing very rapidly, and it is not likely that the growth of the young plants will be rapid enough to pre-

vent their being covered. In the moist sand at the base of the dune shown in *fig. 9* patches of algæ have been seen, presumably Chlamydomonas, such as have been described in connection with the lower beach. It is doubtful if these algæ are of any significance in the capture of dunes.

If the vegetation gets a foothold at the base of an advancing slope, it tends to creep up the slope by means of vegetative propagation. At the base of the cottonwood dune shown in *fig. 5*, there may be seen grasses which appear to be creeping up the slope in this manner. It should be borne in mind that such appearances are often deceptive. In this particular instance the appearance would be the same if the dune were advancing and the grasses rising to keep above the sand. In like manner there is doubt with regard to *fig. 16*, as to which vegetation antedates the dune and which is subsequent. As has been already stated, the clump of dogwoods and willows at the center beyond all question antedates the dune; so too, the dead half-buried pines. The annual bugseeds toward the base, of course, are subsequent.

The greatest doubt is as to the frost grape, *Vitis cordifolia*[4]. At the upper right hand there is a luxuriant grapevine climbing over a dead pine. The clumps back of the willows and the trailing vines in front of them are also Vitis. *Fig. 15* shows several large grapevines back of the row of willows. The coarse-leaved vines at the lower right hand of *fig. 10* are also Vitis. It seems incredible that the vines in this last picture should be anything else than subsequent, since the height of the sand above the wooded hollow is more than twenty meters. Then too the Vitis vines are very abundant all along the coast on the naked dunes, but are rarely found elsewhere. On the dune shown in *fig. 15*, for instance, there are two willows, a dogwood, and the grape growing together. The dogwood and one of the willows are very common in the adjoining swamp, while the grape was not found there at all. On the other hand, no grape seedlings have as yet been found in any such location. While much further study is

[4] The identification here may be questioned; fruiting specimens are rather rare, but prove to be this species so far as examined.

needed in this connection, it seems likely that Vitis is subsequent to the dune.

A little above the center to the left in *fig. 16* is a young cedar, *Juniperus Virginiana*. This little plant is several meters up the slope and is unquestionably subsequent. In the left foreground of *fig. 10* is a shrub of the chokecherry, *Prunus Virginiana*, which is certainly subsequent to the dune. In fact this shrub is rather frequent in such locations. The author does not feel clear as to the conditions which permit the germination and development of these plants in such unstable situations, for it must be remembered that the advance is rather rapid in all cases. No seedlings of the cherry, grape, or cedar have been seen in any such location. It may be that the germination and early growth took place when there was a temporary lull in the advance or during extremely moist seasons. The question cannot be fully solved without a careful study of marked plants for several seasons.

So far as the capture of the dune is concerned, it is a matter of no moment whether the vegetation is antecedent or subsequent. All contribute together to the common end. Of the plants mentioned thus far, Corispermum (shown in the left foreground of *fig. 12*) is of no value in dune capture, because of its annual habit. *Prunus Virginiana* and *Populus monilifera* are rarely abundant enough on lee slopes to be of much value, especially because they have little or no vegetative propagation. The only plants which seem to thrive and increase their area of control on rapidly advancing lee slopes are *Salix adenophylla* and *glaucophylla*, *Cornus stolonifera*, and *Vitis cordifolia*. None of these, however, flourish except on the protected slopes. They are unable to grow along the crest, and hence unable to check the constant advance of the sand.

Vegetation seems to be unable, then, to capture a rapidly moving dune. No such dune has been seen where the vegetation has secured a greater foothold than is represented in *figs. 15* and *16*. This dune is in no sense captured; indeed, its progress is scarcely checked. The more vigorous plants may retain an uncertain foothold for a long time, and again they may not.

So long as the crest is unoccupied by plants, the advance will continue almost without hindrance. The life conditions at the crest are so much more severe than on the slope that vegetation is almost certain to be excluded until the advance is checked by physical agencies. For the capture of a rapidly moving dune, a plant species should have the power of rapid germination possessed by the bugseed, the power of vegetative propagation possessed by the willows, the capacity for growth in height possessed by the cottonwood, or even more than that. The growth of the young plant during the first season should be greater than any of the above, so as to more than counterbalance the vertical component of advance during the period of rest. The life cycle should be of very great length. The plant should be able to endure all extremes of heat, cold, and drought, and all degrees of covering by the sand. No plant species in the Lake Michigan region begins to meet all of these requirements, and, as a consequence, the dunes would advance indefinitely so far as vegetation is concerned.

Various physical conditions tend to check the progress of many dunes. As a dune advances farther and farther from the lake, the effective power of the wind which moves it becomes reduced. The energy is largely spent before the crest of the advancing dune is reached, because of inequalities in its path. The wind commonly builds up other dunes between the lake and the main crest; these dunes serve as barriers, and of course check the advance. Occasionally there are hills in front of the advancing dunes; these check the advance temporarily, at least. The primary cause for a permanent decrease or cessation of movement is the decrease or entire loss of available wind energy. Many wandering dunes never advance rapidly at any period of their life-history. This is because their movement is in some other direction than that of the prevailing wind, or because the full force of the prevailing wind is not directed toward their advance, because of physical reasons. Dunes of this slowly moving type are much more common than the other, and may be seen at almost any point along the entire southern and eastern shore.

Whatever the cause, a slowly advancing lee slope is soon captured by vegetation. The process begins just as described above. Vegetation gets a foothold at the base and creeps up the slope. Antecedent plants, like dogwoods and willows, increase their area by vegetative propagation. Annuals, biennials, and even the hardier perennials germinate and successfully develop at all points. There are many plant species whose power of vertical growth is greater than the vertical component of a slow dune's advance. This latter condition is always the chief test which determines the vegetation of a lee slope. As the advance becomes slower, more and more plant species are able to get and retain a foothold on the dune.

The capture of lee slopes by vegetation was well seen in all its stages at Glen Haven and Grand Haven. At first the vegetation may be dominantly antecedent, as in the case at Dune Park. More commonly, however, the vegetation is chiefly subsequent from the start, chiefly because the area that is encroached upon contains no plants that are fitted for a dune life. Where there is no antecedent vegetation, the first plant to get a foothold is commonly *Ammophila arundinacea*. Plants that follow in quick succession are *Asclepias Cornuti*, *Equisetum hyemale*, *Calamagrostis longifolia*. Some dunes are almost completely covered with a dense growth of Ammophila. All of these plants are perennial herbs and all but Calamagrostis have very extensive vegetative propagation, so that the capture of a slowly moving dune is a relatively quick process. With these plants there may grow annuals and biennials, but they are of little or no value in dune capture. The commonest of these is *Corispermum hyssopifolium*.

Before many years have passed shrubs and small trees find an entrance and gradually drive out the herbaceous vegetation described in the preceding paragraph. These herbs are all fitted to grow in the most exposed situations, but are not adapted to shade. The shrub vegetation of arrested lee slopes may be partly antecedent, but not largely so. The most common species of shrubs on recently captured slopes are *Cornus stolonifera* (or *C. Baileyi*), *Salix adenophylla* and *glaucophylla*, *Vitis cordifolia*,

and *Prunus Virginiana*. With these shrubs young trees of *Tilia Americana* are common. A lee slope thicket of Cornus, Tilia, and others of the above plant species is shown at the upper left hand of *fig. 10*.

All of the species named above occur on arrested lee slopes along the entire coast. The species which are peculiarly characteristic of such habitats are Cornus, Prunus, Equisetum, and Asclepias. These four species are found in other associations, but reach a decided climax here. Ammophila, Calamagrostis, Corispermum, Salix (both species), Vitis, and Tilia are almost as common, but have a much wider habitat range. Ammophila, Calamagrostis, and Corispermum are also found in nearly all plant societies thus far discussed, but they disappear entirely as soon as the vegetation becomes dense. The willows are common in many places on the beach and complex, but they too are ruled out as soon as a real forest vegetation gets a start. Vitis grows also on rapidly moving lee slopes, and remains after the forest has begun. Tilia more than all others looks to the future; as will soon be shown, it is the dominant tree of the first forests that grow on the old lee slopes. With the entrance of the basswood, the true dune conditions and the true dune plants are obliged to pass away.

There are other interesting plants that get an occasional foothold on the arrested lee slopes. At several such places at Glen Haven *Betula papyrifera* was seen. Near Chicago this tree does not grow on the dunes at all, although common along the margins of sloughs. It appears to become more xerophytic northward. Exactly the same is true of *Thuya occidentalis*. Possibly the climatic conditions northward are such as to permit plants that grow normally in protected situations to grow where the exposure is much greater. On an arrested dune at Glen Haven where shrubs for some reason are infrequent, *Solidago humilis Gillmani*, *Aster laevis*, and *Achillea Millefolium* grow abundantly with the herbs previously mentioned.

Before tracing the further growth of vegetation on lee slopes, something may be said of the origin and development of vegeta-

tion within the dune-complex. Of course all antecedent vegetation has been long ago destroyed. The capture of the dune must, therefore, be effected entirely by means of plants which germinate and develop on the complex itself. Speaking broadly, the complex is almost entirely composed of windward and leeward slopes. Since the windward slopes are low, it follows that they cover a much larger area than do the other. Perhaps nine tenths of an ordinary dune-complex is directly exposed to the prevailing wind. The capture of any portion of the windward slope is unlikely, because of the combination of exposure and instability of soil. In the summer a somewhat extensive vegetation may develop, made up largely of annuals and biennials. The most abundant of these plants is *Corispermum hyssopifolium*. Other species are *Artemisia Canadensis* (or *A. caudata*), *Cakile Americana*, *Euphorbia polygonifolia*, *Cnicus Pitcheri*. These plants are commonly more abundant in the deeper wind-sweeps than elsewhere, probably because the sand is moister and more stable in the sweeps than at other places. *Fig. 7* shows a very characteristic wind-sweep with its vegetation composed of the bugseed and other short-lived plants.

Although the summer winds are much less severe than those of winter, the effects on the vegetation of the wind-sweeps are often conspicuous. Artemisia and Corispermum plants frequently have the sand blown away from their roots and they are thus obliged to lean over on the sand. The stems become much twisted and the whole plant is shorter and more compact than when developed in more protected habitats. Occasional perennials that may germinate in such places rarely live over the winter. The vegetation develops anew each year and no steps toward capture are taken. The conditions on the lee slopes of the complex are much like those on the main advancing slopes. Of course all of the vegetation is subsequent. The conditions are, perhaps, more severe because more uncertain. Large slopes covered with Ammophila are common on the Glen Haven complex. Permanent capture may sometimes result on such slopes, but it is much rarer than at the slowly advancing edges of the complex.

FIG. 18.—Lee slope on the dune-complex at Dune Park, captured by the long-leaved willow, *Salix longifolia*, and the cottonwood (broad-leaved forms). Dense clumps of the willow due to vegetative propagation.

The most important development of vegetation on the complex is in the "blowouts," or hollows produced by the wind. These depressions sometimes reach down almost to the water level and may be as much as thirty meters below the general level of the complex about them. In these depressions the sand is moist and protected from the severest action of the wind, so that seeds find ready lodgment and a favorable opportunity for germination and growth. The commonest plants observed are the annuals and biennials mentioned just above, and the following perennials: *Populus monilifera*, *Salix longifolia*, *adenophylla*, and *glaucophylla*, *Juncus Balticus littoralis*. Seedlings of the cottonwood and the three willows appear by the thousand, and a large number survive the rigors of the winter. This is the one dune habitat where Juncus and *Salix longifolia* are at all abundant. These two species are marvelously well adapted to inaugurate dune capture. Both of these plants have very extensive powers of vegetative propagation. Rootstocks of this last-named willow often trail along in the sand for ten, twenty, or thirty meters. Thus the plants extend their area up the slopes of the depression on all sides by means of this vegetative increase. *Fig. 18* shows a lee slope on the complex, which has been almost entirely captured in this way. The dense clump of narrow-leaved shrubs at the center is *Salix longifolia*, probably all coming from one or two plants that have spread vegetatively. The broad-leaved shrubs and trees are *Populus monilifera*.

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[*To be concluded.*]